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I.—THE INTERNAL STRUCTURE OF SOME WESTERN AUSTRALIAN CRETACEOUS BRACHIOPODS.

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I. INTRODUCTION.

The existence of Cretaceous strata in Western Australia has been known since the middle of last century, the best-known and most fossiliferous deposit being the Gingin Chalk, from which numerous organic remains have been described; the best list of references is found in the general account of the formation by Glauert (1910, 1925). The discovery of the free crinoids *Uintacrinus* and *Marsupites* (Withers 1924, 1926), which mark a definite horizon in the European Upper Chalk (Senonian) and have a very wide distribution, the latter occurring in the Upper Cretaceous of all five continents and the former in three of them, fixes the age of the Australian formation as Santonian (Middle Senonian), a global correlation permissible with these non-sessile organisms.¹ More recently Clarke and Teichert (1948) have described the outcrop about 250 miles north of the Gingin district, of a similar chalky bed, the Toolonga Chalk, which yielded a very similar fauna including the zonal crinoids, and which appears to represent another portion of the same Senonian off-shore littoral. The writer, interested in the discovery in this second area of the brachiopods already described by Etheridge (1913) from the Gingin Chalk, and in the resemblance of the Murchison House Series (to which the Toolonga Chalk belongs) to the familiar Cretaceous succession in the South of England, communicated with Professor Clarke, who readily and generously entrusted a quantity of Senonian brachiopod material from Western Australia to him for study. It is mostly on this collection that the account given below is based. All three species studied, when dissected to reveal the internal structures, yielded results of considerable interest, and the palaeogeographic significance of the new generic determinations is discussed accordingly.

(1) See Sieverts (1927) for discussion on the locomotion of living free crinoids with special reference to *Marsupites* and mention of *Uintacrinus*.

II. DESCRIPTION OF THE SPECIES.

Family **TEREBRATULIDAE** Gray.

Genus **INOPINATARCULA** gen. nov.

(Reference is to the homoeomorphy with *Trigonosemus*)

Biconvex capillate terebratulids, with stout cardinalia, stout hinge-teeth with swollen bases, and wide loop.

Inopinatareula acanthodes (Etheridge).

Plate II, figs. 22-27.

1913. *Trigonosemus acanthodes*: R. Etheridge fil. *Bull. Geol. Surv. W. Australia*, No. 55, p. 15, pl. 2, figs. 1-4.

Diagnosis.

Shell about 22 mm. long, 22 mm. wide, and 11 mm. thick; biconvex, rounded-pentagonal, spinose-capillate, anterior commissure uniplicate. Test thick, very finely punctate. Umbo short, suberect, truncated; foramen very small, circular, permesothyrid; symphytium rugose, area concave, hinge-line subterebratulid; stout hinge-teeth with grooved swollen bases, interior of beak greatly constricted, pedicle-valve muscle marks deep and heartshaped. Cardinalia strong; inner and outer socket-ridges, crural bases and outer hinge-plates present; cardinal process transverse; loop, short, wide with arched transverse band; brachial-valve muscle-marks both raised and depressed.

Hypotypes.

Thirty-two specimens in the collection of the Geol. Dept., University of Western Australia.

Description.

(a) External. This flattened terebratulid, which attains a length and breadth of 22 mm. in the series examined, is most commonly rounded pentagonal in outline, with sides formed by the shoulder-slopes, curved lateral commissures and anterior commissure; a minority of individuals show a terebratulid hinge-line instead of the normal subterebratulid one, so that the maximum width occurs anterior of the normal position at half the shell-length, with consequent alteration in the outline. In young shells (length 7 mm.), the anterior curve runs in a half circle from the shoulder slopes, the pentagonal outline being eventually attained at about 14 mm. shell-length. The commissure is markedly uniplicate in the adult; this feature is feebly developed in the 7 mm. examples and accentuates during subsequent growth to a wide rounded curve in the adult, occasioned by a broad median plica in the brachial valve opposed by a similar sulcus in the pedicle valve. In occasional examples this fold rises so steeply that the shell becomes selliform. Both valves are densely capillate from umbo to margin, new capillae arising both by intercalation and bifurcation, and very occasionally reuniting: at the margin of an adult specimen about four such rounded capillae with three flattened interstices occupy 1 mm. Sporadic lines of interruption of growth, sometimes step-like, cross the capillae which are irregularly set with small scattered spinose projections. These spines are only visible on well-preserved specimens, and are most densely set around the umbones, on the earlier formed portion of the shell; as growth proceeds they appear more sparsely, though there is considerable variation in this respect. The test is very finely punctate, the punctae being only visible with a magnification of about x20.

The pedicle-valve palintrope is concave, and is bounded by the cardinal margin and by the two beak-ridges meeting at the pin-hole foramen just below the apex. The symphytium is in the form of a low equilateral triangle and shows well-marked transverse growth-lines, and is bounded by narrow ill-defined interareas; outside these, to left and right, the remainder of the palintrope shows the continuation of pedicle-valve growth-lines across the rounded beak-ridges. The height of the palintrope is about one eleventh of the shell-length in the adult.

(b) Internal: pedicle valve. The interior of this valve is smooth, rising along the anterior-posterior mid-line as the internal expression of the external median sulcus which commences inconspicuously and widens to the anterior commissure. Posteriorly the anterior of the umbo and region of the hinge-teeth are very heavily calcified, the symphytium being fused to and covering a solid umbo perforated only by a thread-like tunnel leading down from the pin-hole foramen; this tunnel emerges as a narrow notch sloping steeply down to the posterior point of the muscle-area described below. Left and right of the notch the walls of the calcified foundations of the hinge-teeth curve anteriorly and outwards and diverge. The hinge-teeth, large and massive, lie to left and right anterior of the corners of the symphytium, and are deeply notched half-way between the floor of the valve and the tops of the teeth. These notches widen posteriorly to spoon-like depressions, and the socket-ridges of the brachial valve interlock in them. Externally the teeth are delimited from the edges of the valve by narrow grooves.

The muscle-marks form a heart-shaped area, widening anteriorly from the calcified umbonal structures and terminating at about a third of the shell-length. They are deeply marked and visible as a translucent area on the opaque shell. This area is divisible into separate muscle-scars. At the foot of the pedicle-notch a raised tongue—or teat-shaped deposit of callus points anteriorly; immediately anterior of this is an elongate median paired scar.

Two large fimbriate scars occupy the anterior portion of the whole area, and there are two poorly defined lateral scars. These last occupy the position of the main pedicle-muscles in some living brachiopods: the large scars apparently represent the diductors, the median paired scar the adductors, though it is small for this purpose, and the tongue-shaped callus possibly the attachment of the subsidiary pedicle-muscle. Successive growth-attachments of the supposed adductors within the median scar show as concentric lines.

All these details of the pedicle-valve are best seen on adult specimens in which the median fold is only moderately developed.

(c) Internal: Brachial valve. The interior of the valve is smooth, marked by a median antero-posterior depression of variable development, the opposite feature to the median fold seen within the pedicle-valve, and usually less prominent owing to the brachial valve being flatter. The cardinalia are well-developed, and various separate structures are distinguishable. The sockets are wide and triangular, the callus which floors them forming slight rounded outer socket-ridges immediately within the valve-margins; on the inside, the sockets are overhung by high massive inner socket-ridges which are externally visible in a posterior view of the valve like the hinge-projections in *Terebratulina*, overhanging the outer socket-ridges near the umbo. On the inner side of the inner socket-ridges, the slopes are obliquely downward and concave to two sharp edges, divergent from the umbo: these

edges are undercut by the steep wall-like descent of the solid divided cardinalia, either side, to the floor of the valve, the loop being attached to the walls. The concave surfaces are interpreted as outer hinge-plates, though not shelf-like anteriorly as is typical for this structure, and the inner edges as crural bases, from the loop-attachment. The transverse cardinal process is situated just inside the umbo and shows a posterior concave roughened surface and a smooth anterior bulbous surface above the descent to the valve-floor, the two surfaces separated by a denticulate edge. The loop is wide and short; from the crural bases the upper edges of the ribbons curve inwards to form the curve, the ribbons themselves diverging anteriorly at about 26° from the midline to about one third of the length of the valve and then curving upwards and backwards to form a transverse band so broadly curved that the two side-slopes are much closer to the descending branches than to each other.

All these structures are naturally best seen on mature specimens, but it should be noted that the immature loop in a brachial valve of 7 mm. length is proportionally much narrower than the adult loop.

The muscle-marks of the adult valve show two deep and conspicuous pyriform scars whose rounded anterior terminations are a little short of the half-way position along the valve-length. These scars are each sub-divided by a transverse ridge. Between them is a raised platform of callus extending forwards from the sharp descent within the umbo. The pyriform scars are interpreted as adductors; the pedicle-muscles could have been attached either to the median callus or to the hinge-plates.

Remarks.

Inopinatarcula is a distinctive terebratuloid which does not suggest close affinity to any form known to the writer. The loop is somewhat similar in general appearance to that of *Aguehasia* as figured by Davidson (1886, pl. 7, fig. 3), but this little genus differs very much in size, characters of the beak, etc. The Australian shell is easily distinguished from the European *Trigonosemus*, to which it was first referred, by the coarse costate ornament and much higher area of the latter, which has a very different internal structure with massive cardinal process, strong median septum and long loop. The classification of the Terebratulidae or short-looped forms is at present unsatisfactory, but there can be no doubt of the distinctness of the present form nor of its claim to generic rank.

Family **DALLINIDAE** Allan, 1940.

Subfamily **KINGENINAE** Elliott, 1948.

Genus **KINGENA** Davidson, 1852.

Kingena mesembrina (Etheridge).

Plate I., figs. 1-13.

1913 *Magas mesembrinus*; R. Etheridge fil., *Bull. Geol. Surv. W. Aust.*, No. 55, p. 15, pl. 2, figs. 5-8.

Diagnosis.

Shell about 18 mm. long, 16 mm. wide and 9 mm. thick, biconvex rounded pentagonal to elongate-oval, test thin, externally finely granulose and conspicuously punctate, anterior commissure feebly sulcate. Umbo short, sub-erect, truncated; foramen moderately large, circular, permesothyrid; deltidial plates disjunct and obscured by the beak-ridges, hinge-line terebratulid.

Hinge-teeth supported by dental lamellae, joined by sessile pedicle-collar. Cardinalia showing strong fused inner socket-ridges and crural bases, wide hinge-trough and transverse cardinal process; kingeniform loop supported by a short median septum. Muscle-marks and pallial sinuses faint.

Hypotypes.

Twenty-one specimens in the collection of the Geological Department, University of Western Australia: eight specimens in the collection of the Perth Museum.

Description.

(a) External. This shell varies somewhat in outline, though easily recognisable. Specimens which are rounded pentagonal in outline include the largest individuals. This type is thin-shelled, the fossils often being crushed; and the commissure, if sulcate, is very feebly so, showing some tendency to ligate opposite folding; there are no marked lines of interruption of growth. The other type is slightly thicker-shelled, elongate-oval in outline, and shows slight but definite sulcation. The test for the species as a whole shows on well-preserved shells the fine external surface granules characteristic of the genus; the punctation is coarse but regular and close-set. Some shells show faded orange-brown or reddish colouration: this was recorded by Davidson (1852, p. 45) for English *K. lima*; and the living *Laqueus* and *Frenulina*, with loops similar to *Kingena*, are often attractively coloured. The greatest thickness of the pedicle-valve occurs at half the shell-length, but the corresponding dimension of the brachial valve occurs at about one-third of the valve-length anterior of the umbo. The internal median septum is externally visible as a dark streak for two-fifths of the length of the brachial valve. At the umbo, short and suberect, the foramen, moderately large and circular, is seen to be permesothyrid in position; the beak-ridges, strong at the umbo, fade out quickly to left and right. In most specimens these beak-ridges are close to and obscure the area above the dorsal umbo, but in young examples two disjunct triangular deltidial plates are seen, and one such example showed these bordered by narrow interareas, with the remainder of the palintrope showing transverse growthlines to left and right below the beak-ridges.

(b) Internal—Pedicle-valve. The hinge-teeth lie at the outer corners of the delthyrium, and are supported by clearly-visible dental lamellae, nearly vertical, the bases on the valve-floor being slightly closer than the upper limits immediately under the teeth, and leaving clear cavities anteriorly between the lamellae and the sides of the valve; posteriorly (towards the umbo) the lamellae are somewhat convergent. On the floor and sides of the beak-interior is a thickish sessile pedicle-collar, covering or passing into the dental lamellae up to the deltidial plates. Anteriorly the termination of the collar is clearly-marked, forming a posteriorly curved step between the two lamellae, so that its median length is shorter than at the sides. It shows concentric growth-lines parallel to the anterior margin.

The muscle-marks are obscure, forming an oval patch immediately anterior of the pedicle-collar. Faint but more prominent are four anteriorly radiating lines, an inner pair left and right of the muscle-marks, and then an outer pair; these are traces of the main pallial sinuses.

(c) Internal—Brachial valve. In this valve the cardinalia are simple but distinctive. To left and right the valve floor rises to the rounded edges of the curved anterior margins of the socket floors, which separate from the valve-floor inwardly, so that the cardinalia are undercut. At the same time these anterior socket-margins curve upwards, are joined by the crural bridges of the loop, and thicken to overhang the sockets and to extend posteriorly as prominent inner socket-ridges meeting the valve margin left and right of the umbo; there are no distinct outer socket-ridges. Immediately within the umbo the cardinal process shows as a transverse, very low-equilaterally triangular concave surface, but without any swollen surface below its anterior edge. A stout rather low median septum joins the cardinalia anteriorly and spreads into a conspicuous wide concave hinge-trough which lies between the cardinal process and the inner slopes of the inner socket-ridges proper. The floor of the hinge-trough is anteriorly free of the valve-floor in continuation of the socket-floors and is supported by the median septum. This is the normal pattern of cardinalia seen in young and adult shells. In the largest example examined, however (length of brachial valve 18 mm., shell-length 21 mm.), well-defined hinge-plates are seen on the insides of the socket-ridges, the septum running in at a lower level some distance before passing into a steep slope up to the cardinal process. Presumably the pedicle-muscles were normally attached to the inner slopes of the socket-ridges, and with increasing curvature of the umbonal portion of the valve during growth in this old specimen the slopes become converted to shelves or true hinge-plates, the hinge-trough proper becoming merely the posterior slope described above. The phenomenon is of some interest since normally the details of the cardinalia, unlike those of the loop, individualise during growth without definite appearance of new structures. Unless such old individuals are commoner than the collection studied suggests, hinge-plates should not be considered characteristic of the species.

The loop is typically kingeniform (Ref. Davidson, 1852, p. 41). From the cardinalia the crura extend anteriorly, giving rise to crural processes of moderate length curving inwards: the descending branches run forwards, outwards and downwards, and on their inner sides widely-attached connecting bands narrow inwards and connect them to the septum. The descending branches then curve upwards and inwards in a wide sweep, running back as ascending branches to turn inwards and meet in a very wide high transverse band, almost vertical to the floor of the valve. This transverse band continues downward as two inward and backwardly (anteriorly) curved connections to the median septum, joining it above the connecting bands from the descending branches and within the curve sketched by the crural processes, and so leaving a narrow gap in the box-like loop when viewed posteriorly. Laterally the loop resembles a butterfly with raised folded wings; anteriorly two pairs of connections to the septum are clearly visible one above the other within the recurved loop-bands. The descending branches are fringed externally with short spines, and anteriorly near the points of recurvature these spines become long and graceful, especially in young examples.

In adult examples the transverse band shows two angled folds above the vertical connecting bands. Large examples are usually found crushed when dissected.

No unbroken pre-Kingeniform immature loops were dissected; the preparations obtained suggest an earlier dallinid growth-stage with septal

pillar, campagiform hood and descending branches with very wide attachment to the septum and long anterior spurs. The relation of the Kingeniform loop to other dallinid loop-patterns is fully discussed below.

The median septum from the hinge-trough rises to its highest at the points of loop-attachment—the type-figure (Etheridge, 1913, pl. II., fig. 8) shows a broken example without loop—and then rapidly descends to the valve-floor and fades out.

Two indistinct muscle-marks are seen on the valve-floor, left and right of the median septum.

Remarks.

The observed variations in size and shape of *Kingena mesembrina* fall within the extreme limits of variation of the European *K. lima*, a long-range species (Albian-Senonian) probably capable of subdivision; but the characteristic external surface granules are smaller and more closely-set in the Australian species. The oval, thicker-shelled, markedly sulcate forms with numerous lines of interruption of growth, from which Etheridge's type-specimen was selected, are noteworthy, probably representing slightly stunted or slow-growing individuals. *Kingenas* as a rule show slight uniplicate folding, but it is not invariable; sulcate individuals of *K. lima* occur in the British Cenomanian, and *K. granulifera* Stoliczka is figured as sulcate.

The Australian assemblage as a whole represents a distinct geographical species.

K. mesembrina shows the characteristic loop on which Davidson based the genus. The writer, discussing the loop-development of the Dallinidae (1948b, p. 311) pointed out that just as *Laqueus* and *Pictothyris* diverge from normal dallinid development by retention of the frenuliniform connecting bands between ascending and descending branches, so *Kingena* appears to represent a genus parallel to the terebrataliform which had retained its campagiform attachment to the septum, and so was referred to the new subfamily Kingeninae, with the expectation that the loop-development, when known, would confirm this. It is regretted that the present material did not permit observation of the full developmental series, though the broken campagiform loop, and the earliest complete loop, the latter somewhat reminiscent of that seen in a young adult *Frenulina*, are as expected. Meanwhile observations on other genera permit a slightly better understanding of *Kingena*. In the frenuliniform growth-stages both of the North Atlantic Recent *Waldheimiathyris cranium* and the British Cretaceous *Gemmarcula aurea* the posterior connecting bands individualised by the frenuliform lacunae join the median septum above the broad junction of the descending branches. In *Frenulina sanguinolenta* itself, in a small example which has just attained an adult loop, the ground-plans of the posterior connecting bands run obliquely out from the median septum, where they meet, across the attachments of the descending branches; in a larger example the posterior connecting bands are set apart. Finally, in *Laqueus suffusus* the corresponding bands run from the ascending branches to the outside ends (left and right) of the attachments of the descending branches to the septum, but join the latter on the insides of the descending branches. It is not merely changes in the pattern of loop-structure, but proportional and orientational changes during growth, which bring about the final complicated forms of terebratelloid loops, as emphasised by the writer when considering

joint loop-and-lophophore development (*op. cit.*, p. 302). Now in *Kingena*, the progressive separation of the posterior connecting bands seen in the *Frenulina-Laqueus* series has not occurred, the original close attachment of posterior connecting bands separated by the posterior resorbed opening in the hood being retained with proportionally small increase in size, *pari passu* with the development of a very broad transverse band. Thus the frenuliniform lacunae eventually give rise, not to the spaces between ascending and descending branches more or less in one plane of *Laqueus*, but to the gaps with twisted boundaries formed by the descending branches, the connecting bands from these to the septum, the connections from the transverse band to the septum, and the ascending branches, as seen in the adult *K. mesembrina*.

The numerous spines on the loop of *Kingena* are reminiscent of those seen in various Jurassic zeillerid genera, and are met with in varying degree in dallinid genera, surviving in the young of the living *W. cranium*, but they do not occur in terebratellid genera. They are a further indication of the more primitive calcification of Dallinidae as compared with Terebratellidae.

Kingena mesembrina attained its kingeniform loop early: if the length of the shell at which an adult pattern of loop is attained² is expressed as a decimal of the length of the fully adult shell³ the observed result is 0.32, perhaps a little less. This ratio is of interest, since there is good evidence in support of the view that terebratelloid loop-development has been brought about by intra-specific competition for food-supply in crowded brachiopod colonies, with resultant selection pressure in favour of a more efficient lophophore and its earlier attainment, and consequent modification of the supporting loop (Elliott, 1948a, b). Corresponding figures for *Mühlfeldtia truncata* (Linn.), *Terebratella dorsata* (Gmelin), *T. inconspicua* (Sowerby), *Magellania venosa* (Solander), *Neothyris lenticularis* (Desh.), *Waldheimiathyris cranium* (Muller), and *Dallina septigera* (Lovén), all Recent, are 0.33–0.5; for the Recent *Dallinella obsoleta* (Beecher) 0.17.⁴ *Kingena mesembrina* (Etheridge) and *Gemmarcula aurea* Elliott, both Cretaceous, give figures of 0.32 as stated, and 0.5 respectively. All these genera are in loop-pattern at the end or nearly so of their developmental series. For the Recent *Frenulina sanguinolenta* (Gmelin) and the Jurassic *Hamptonina buckmani* (Moore), lower genera in their developmental series, the figure is about 0.8.

Ignoring *Frenulina* and the Mesozoic genera for the moment, the remainder are temperate or cold-water forms, some being found in the cooler waters at considerable depths in lower latitudes. The increase in size of marine organisms in colder waters is a well-known phenomenon⁵; thus Sverdrup, Johnson and Fleming (1942, p. 857) say "Lowered temperatures lengthen the time required for poikilothermic animals to reach sexual maturity. Hence, in cold-water forms the delay permits a longer growing period with resultant larger size at maturity. It has been shown that the oxygen consumption of certain non-locomotory warm-water benthic species is higher than that of related cold-water species with which they were experimentally compared,

(2) This feature is subject to variation (cf. Fischer & Oehlert, 1892, p. 294 and expl. pl. XI.) on shell-size and loop-pattern attained in *Terebratella dorsata*, and the writer on a similar phenomenon with exterior structures in *Gemmarcula aurea* (Elliott, 1947, p. 147) but an average may be obtained for most species.

(3) Shell-length is a simple linear expression, adopted for convenience, of the cubic content of the shell to which the animal and its nourishment are related.

(4) These figures are obtained from published results or single series of specimens: the writer has not had sufficient material for a detailed study of this phenomenon.

(5) For a brachiopod example cf. Wesenberg-Lund (1941 b) on shell-size in *Dallina septigera* (Loven) in the N. Atlantic.

and this difference in metabolism may have a bearing on the question." It is considered here that in the brachiopods under discussion this increase in size and length of life accompanied the progressively more rapid brachiopod lophophore-development with its corresponding effect on the loop, and that the operation of the two factors *par passu*, physical-physiological and biological-genetic, is shown by the small shell-size at which these terebratelloids attain a loop of adult pattern, relative to the maximum shell-size eventually attained. *Kingena* and *Gemmarcula* occur in almost non-coralliferous deposits and may be taken as temperate and listed with the others. *Frenulina*, however, is a warm-water coral-reef species in the Pacific, and the Jurassic *Hamptonina* occurs in a coralliferous deposit⁶; both are small species⁷. It therefore seems possible that the early sexual maturity and more abundant food-supply of those shallow warm-water species which have managed to retain their position in face of molluscan competition (cf. Elliott, 1948c) leads to small size and slower loop-evolution. Further information, particularly on genera with primitive loops is desirable; so little detailed information is available on brachiopod ecology that the unravelling of their evolutionary story, as apart from description of faunas, can scarcely be said to have begun.

Family **TEREBRATELLIDAE** King, 1850.

Subfamily **BOUCHARDIINAE** Allan, 1940.

Genus **BOUCHARDIELLA** Doello-Jurado, 1922.

Bouchardiella cretacea (Etheridge).

Plate II., figs. 14-21.

1913, *Magasella cretacea*: R. Etheridge fil., *Bull. Geol. Surv. W. Aust.*, No. 55, p. 16, pl. 2, figs. 9-12.

1915, *Magadina cretacea*: Etheridge: Thomson, *Trans. N.Z. Inst.*, xlvii., p. 399.

Diagnosis.

Shell about 5 mm. long, 4 mm. wide and 2 mm. thick; biconvex (dorsal umbo flattened), elongate ovoid-pentagonal; test smooth, thick, densely punctate, commissure sulcate; beak short and nearly straight, beak-ridges sharp, foramen epithyrid to permesothyrid, symphytium fused with concave palintrope, hinge-line slightly sloping. Interior of pedicle-valve beak constricted, hinge-teeth stout with grooved swollen bases, muscle-marks anterior, well-marked, separated by median ridge. Brachial sockets deep, cardinal platform solid, socket-ridges prominent, muscle-pit posterior and subquadrate, septum high anteriorly, loop retrograde pre-magadiniform.

Hypotypes.

Sixty-two specimens in the collection of the Geological Department, University of Western Australia.

Description.

(a) External. This little shell, fully adult when it attains the dimensions given above, is smooth-surfaced without marked lines of interruption of growth, though with a magnification of x 12 the growth-lines are seen to be

(6) The doubtfully mature loops figured by Zittel (1870) are from reef deposits.

(7) The Recent species *Kingena alcocki* Joubin, related to *Frenulina*, occurs in deeper water; and is larger, with a loop trending towards that of *Luqueus*.

irregular in prominence. The anterior commissure is markedly sulcate, the pedicle-valve curving to a blunt rounded carina whose slopes fall to the lateral commissures, and the brachial valve to a median sulcus within the normal curvature and anterior of the flattened umbonal-region. In outline the shell is elongate-oval or obscurely pentagonal, the greatest width being a little anterior of the mid-point of the shell length; earlier stages were perhaps proportionately a little wider, and certainly less sulcate. The test is thick and densely punctate. The symphytium, slightly concave, low and wide, appears blended with the rest of the pedicle-valve palintrope, and the whole, showing obscure transverse growth-lines, is bounded anteriorly by the two halves of the sloping hinge-line and posteriorly by sharp beak-ridges. The pedicle-valve beak is short and nearly straight; the foramen, almost at right angles to the plane of the symphytium, normally occupies the termination of the beak and encroaches on the thickness of the beak-ridges at the apex, but sometimes cuts through to notch the symphytium-apex.

(b) Internal—Pedicle-valve. The interior of the beak of this valve is constricted by shell-thickening, though this is in no wise comparable in extent to the same phenomenon in *Inopinatarcula*. The hinge-teeth are stout and the bases merge below into the floor of the valve, constricting the interior of the beak posteriorly and diverging to merge anteriorly into the sides of the valve; half-way up these bases are prominently notched for the reception of the brachial-valve socket-ridges. The hollow of the floor of the interior of the beak gives place suddenly at about one-third of the shell-length to a broad rounded and obscurely double median ridge extending to near the anterior commissure. Left and right of this ridge are two reniform muscle-marks with rounded anterior terminations at approximately three-fifths of the shell-length.

(c) Internal—Brachial-valve. The posterior third of this valve is occupied by a solid cardinal platform. Left and right are wide sockets, without outer socket-ridges: between them is the high cardinal platform proper, trapezoid in plan and narrowing posteriorly to terminate above the valve-umbo; and with rounded outer edges to left and right overhanging the sockets and so corresponding to the inner socket-ridges of more conventional cardinalia. The posterior surface of the cardinal platform shows a shallow, rounded to heart-shaped muscle-pit with several concentric growthlines: the indentation is anterior. The larger anterior portion of the cardinal platform shows two subsidiary antero-posterior ridges lying between the socket-ridges. Anteriorly the cardinal platform falls steeply and is joined at the base by a broad low median septum. On each side of this is a small cave within the vertical face of the hinge-platform, left and right, and there is a third depression, less deep, above the septum.

The septum narrows anteriorly, curves upwards steeply to a high summit with limited anterior extension, then falls vertically to merge at the base in the median ridge corresponding to the external sulcus. From the upper part of the steep posteriorly-facing slope just below the summit, two curved lamellae extend, one each to left and right, narrowing and recurving to point to one another; they vary somewhat in size and curvature in different specimens, and in old individuals become broad curved triangular plates with wide bases on the septum.

Two ill-defined elongate muscle-marks are seen on the valve-floor to left and right of the septum.

Remarks.

This species was compared by Etheridge to the Recent *Magadina cumingi*, then known as *Magasella* and referred by him to the same genus. On the dismemberment of *Magasella* Thomson (1915a, p. 399) referred the fossil to his genus *Magadina* (type-species *M. browni*) as one of several previously-described Australian forms which combined bouchardiform shape with magaselliform loops. The term magaselliform was stated by the same writer (1915b, p. 405) to cover both magadiniform and magelliform loop-patterns. As described above, however, the loop of *B. cretacea* is degraded pre-magadiniform, agreeing with that of *Bouchardia*. The muscle-marks and hinge-platform with anterior caves are also similar to those of *Bouchardia*, but the prominent inverted-V cardinal process of this genus is missing, and indicated only by the anterior indentation of the cardinalian muscle-pit, an early stage in the shift of the diductors from a concave to a convex attachment. This feature is as described for the S. American Cretaceous *Bouchardiella* (Doello-Jurado 1922, p. 200), which is stated to differ only from the Tertiary and Recent *Bouchardia* in the less-advanced cardinal process. If *Magadina browni* (Thomson), *Bouchardia rosea* (Mawe) and *Bouchardiella cretacea* (Etheridge) are compared side by side, the resemblances between all three are obvious, but the Cretaceous fossil is seen to incline towards *Bouchardia* rather than *Magadina*, resembling most closely the young of *B. rosea*. In *Bouchardia* the symphytium is blended with the rest of the palintrope and the foramen is epithyrid: in *Magadina* the symphytium is distinct and foramen permesothyrid. *B. cretacea* shows no distinct symphytium, and in the majority of species the foramen lies between the beak-ridges at the apex (epithyrid), though it may encroach on their thickness: only occasionally does it notch them and so become permesothyrid. *B. cretacea* is smaller and more elongate than the S. American type-series *Bouchardiella patagonica* (von Ihering), but this is only a difference of at most specific rank. The writer regrets that he has not been able to examine figures or specimens of the interior of *B. patagonica*, but the agreement of this feature in the Australian fossil with Doello-Jurado's description of it in the S. American one is so close that the former is here removed from *Magadina* to *Bouchardiella*, bearing in mind that it appears to be a form very close to the ancestral stock for both Magadinae and Bouchardiinae, as might be expected from its geological age⁸. As it possesses a degraded loop like that of the Bouchardiinae it seems unnecessary to erect a new genus for its reception.

Bouchardiella cretacea is thus another example of a terebratellid genus with a very primitive loop. The writer has elsewhere discussed the special ecological conditions considered as the indirect cause of loop-development. It must be pointed out, however, that although the sporadic progress of loop-evolution, due to the repeated confluence of selection-pressure and growth-rate mutation, might be supposed to average out the numbers of genera in each stage of development or bring them all to the final stages, this is not the case. Thus *Bouchardiella* is one of numerous primitive terebratellids with pre-magadiniform and magadiniform loops, modified as described above by reason of their permanence. No such variety exists in the primitive dallinids where the more primitive calcareous hood (as compared with the terebratellid ring) are rapidly modified, and only *Campages*⁹ survives with a modified hood. The intermediate magelliform or frenuliniform stages are rare in either

(8) Cf. Thomson . . . " it is probable that *Bouchardia* is a retrograde genus from a forerunner of *Magadina* . . ." (1915a, p. 402), and " it is probable that in loop characters *B. rosea* is degenerate from stock originally possessing pre-Magadiniform characters " (1915b, p. 406).

(9) The writer has not been able to examine a specimen of *Jolonica*.

series, since the former passes imperceptibly into the terebratelliform, and in the latter the frenuliniform bands are easily resorbed or diverge during growth to give a terebrataliform or laqueiniform stage. Finally, the numerous terebratelliform and terebrataliform species indicate that these stages, like the premagadiniform and magadiniform, are more permanent and that further resorption is not essential. This is confirmed by the fact that during the development of *Dallina septigera* the terebrataliform stages persist through an increase in shell-length equal to the previous growth of the shell up to that stage (Fischer Oehlert, 1891); a similar state of affairs is indicated with the terebratelliform stage in *Neothyris lenticularis* as figured by Davidson (1886, pl. IX, figs. 10-13). Thus even when evolutionary progression is continuous it is likely to be irregular.

III. PALAEOGEOGRAPHIC SIGNIFICANCE OF THE FAUNA.

It remains to consider the significance of the presence of these three forms in the Senonian of W. Australia. The supposed occurrences of *Magas* and *Trigonosemus*, terebratellid genera found in the Upper Senonian of Europe, accompanied by *Magadina cretacea*, an early representative of a typically Tertiary Australian family has been taken as evidence supporting the origin of the Terebratellidae in the northern hemisphere, and migration to the Australasian region via the Tethys. Since the European and Australasian beds in question are of much the same age, the Terebratellidae might on these grounds have originated anywhere along the Tethys, migrating in both directions; however, *Magas* and *Trigonosemus*, as shown above, are erroneous determinations for the Australian species. Moreover, there is other European evidence to be considered. *Magas* and *Trigonosemus*, referred to the Terebratellidae by reason of their loop and cardinalia respectively, appear suddenly in the Senonian of W. & N. Europe¹⁰, accompanied in Scandinavia by *Rhynchora* and *Rhynchorina* which are stated to have *Magas*-like loops by Eudes-Deslongchamps (1884) and Oehlert (1887) respectively¹¹ and presumably spreading during the period of reduced selection-pressure consequent on the extensive and continued marine transgression in this region¹². Previous to this, there are doubtful records of *Magas pumilus* from Cenomanian and Turonian (Jukes-Brown 1904), various species referred on external form alone to *Magas* and *Trigonosemus* (e.g. *M. geinitzi* Schloenbach and *T. incertus* Davidson from the Cenomanian), and the genus *Terebrirostra* similarly referred to the terebratellidae on account of its cardinalia and ranging from Neocomian to Cenomanian. An investigation of the internal structure of these and other doubtful forms, and if possible of their loop-development, is necessary to settle this question; meanwhile the balance of such evidence as is available does support a European origin for the Terebratellidae.

Dealing now with the three Australian forms in the light of the new evidence, *Inopinatarcula* is a new form and whilst adding to the variety of described forms possesses no palaeogeographic significance as yet.

Bouchardiella cretacea is a southern form. The distribution of the brachiopods from the Recent and Tertiary of the Southern hemisphere was exhaustively discussed by Thomson (1918, p. 58), who concluded that "The dis-

(10) *Trigonosemus* sp. occurs in the Senonian (probably Maestrichtian) of N. Turkey. Record by courtesy of the Directors and Chief Geologist, Messrs. Iraq Petroleum Co., Ltd., London.

(11) Cf. also *Morrisia ? suessi* Bosquet and *Terebratella decorata* and *T. Lujani* Vidal, from the Maestrichtian of Belgium and Spain respectively.

(12) For an illustration of the reverse phenomenon in this region during early Tertiary times ref. Elliott (1948c).

tribution of Southern Recent brachiopods . . . is satisfactorily explained by an ancestral distribution in the Miocene . . . The generic similarities between the four southern Oligocene-Miocene faunas¹³, on the other hand, are of such a nature as to demand at some earlier date much greater means of inter-communication between the lands bordering the South Pacific Ocean than exist at the present day. So far as the genera are concerned they might have occurred as far back as the Cretaceous . . . ”

As explained above, *B. cretacea* agrees with the Patagonian *B. patagonica* in structure and geological age and they are Upper Cretaceous representatives of a considerable fauna, mostly Tertiary. The reference of the Australian fossil to *Bouchardiella* here is a matter of convenience, and it appears to be a form very near the ancestral junction of Bouchardiinae and Magasinae. Whether such forms had spread from Europe to escape extinction and give rise to the higher Terebratellidae in Southern seas must remain unknown, but it is at least possible. *Tanakura* and *Nipponithyris*, from the Miocene and Recent respectively of Japan, presumably indicate a Tertiary northward Pacific migration, much as *Waldheimiathyris* (*Macandrevia auct.*) has migrated Southwards through the post-Miocene Pacific to the Antarctic (Thomson 1927, p. 241), but the doubtful little terebratelloid described by the writer from the French Eocene (Elliott 1940) may possibly be a European post-Cretaceous survivor. Whether the S. American and Australian species represent two forms of many along the Gondwanaland coast, surviving to our notice by reason of the present non-submergence of the rocks in which they occur, or whether some degree of continental drift accounts for their present wide separation, is beyond the scope of this paper. The writer, in W. Europe, has found little need to invoke the agency of continental drift, but better acquaintance with the problems of the Southern hemisphere, where the widely-separated land-masses show close stratigraphic and faunal resemblances, even with animal parasites (ref. Eichler, 1949), might change his views.

Kingena mesembrina offers evidence of a different kind, and extends the geographical distribution of this genus to all five continents. Species have been referred to *Kingena* from Jurassic, Cretaceous, Eocene and Recent. Of these, the Jurassic forms are probably not *Kingena*, e.g., the Lebanon fauna described by Krumbeck (1905)¹⁴, and *K. raincourti* E.-Desl. and *K. constantinensis* Cossm. and Pizarro, very rare in the French Eocene, are possibly post-Cretaceous survivors, possibly new forms. Investigation of the internal structure is necessary to confirm the final reference of all these fossils to a genus. The recent *K. alcocki* Joubin has been shown to be a related form to *Frenulina* and *Laqueus* (Jackson 1921; Thomson 1927, pp. 242-43). In the Cretaceous, the variable *K. lima* (Defr.), the type-species, ranges from Albian to Senonian in Europe, and neither Davidson (1852, pp. 43-44) or Eudes-Deslongchamps (1887) could decide on its separation into stratigraphical species, though this is no doubt possible with the aid of statistical population-studies, as with certain large foraminifera; e.g., Henson (1948) on *Orbitolina*. Other Cretaceous forms recognisable as *Kingena* by the external form, surface ornament where preserved and beak characters are *K. wacoensis* (Roemer)¹⁵ common in the Texan Cretaceous, N. African records of *K. lima* (Peron 1893, Daque 1903), *K. umbaghghikensis* Shalem from the Dead Sea area in

(13) Australia, New Zealand, S. America, Antarctica.

(14) See also Muir-Wood (1935) on *Zeillera latifrons* (Krumbeck).

(15) Loop figured by Cooper, in Shimer & Schrock (1944).

S.W. Asia, and the Indian species described by Muir-Wood (1930) from the N.W. and Stoliczka (1872) from the S. To these may be added the present Australian species.

If the geographic location of the above is considered it is seen that they all occur closely to the Tethys, being distributed by the world-wide marine transgressions of the upper half of the Cretaceous, from the Albian onwards. Of the Australian brachiopods considered, then, *Kingena* is the link with other areas: its occurrence in Australia fitting in with a probable lower Cretaceous origin and upper Cretaceous dispersal. It does not add to the zonal information furnished by *Marsupites* and *Uintacrinus* but the world-wide dispersal of a brachiopod belonging to a type with very limited larval opportunities for dispersal does indicate exceptional opportunities for migration, for whilst such slow migration is rapid in comparison with sedimentation, there are usually land and deep-sea barriers to prevent wide brachiopod dispersal (cf. Thomson 1927, p. 47). Such opportunities, in the present state of our knowledge, are best indicated by the Cretaceous Tethys and its transgressions.

IV. FURTHER NOTES ON TEREBRATELLOID EVOLUTION¹⁶.

Since the writing of this account some additional evidence has come to hand. The statement of Thomson (1927, p. 289) is quoted in support of the strictly local development of loop-progression "*Neothyris* is merely a *Pachymagas* which has attained the magellaniform loop stage," and he points out that in New Zealand species of the former suddenly replace those of the latter, with but one exception, at one Oligocene horizon, and only *Neothyris* survives in the Pliocene: whilst in Patagonia *Pachymagas* survived till the Pliocene and apparently did not give rise to *Neothyris*.

This local development was considered to be due to the crowded terebratelloid brachiopod communities, consequent upon limited opportunities for larval migration (cf. Blochmann, 1908, on the Norwegian species). Additional evidence on this point may now be given from the Scandinavian region. Detailed studies of the plankton of the fjords (e.g., Runnström, 1932) have confirmed the absence of the larvae of the bottom-living brachiopods in the higher layers of water. In the elaborate and detailed study of the planktonic larvae of bottom-living animals in the Danish Öresund by Thorsson and collaborators (1946) no trace of brachiopod larvae was found, although a substantial proportion of the larvae are swept in by the bottom current from the Kattegat and even from the more distant Skagerrak to the North, and at least one brachiopod species is known to occur as far south as the former (Wesenberg-Lund, 1941a). This latter writer refutes the one record of an adult brachiopod from the Sound as a probable error (*op. cit.*, p. 4). It seems clear, therefore, that only very limited opportunities for terebratelloid larval dispersal exist normally when compared with some other invertebrates. Whether the ability to delay metamorphosis pending discovery of a suitable ground anchorage, as in certain polychaetes (Day & Wilson, 1934: Wilson, 1937, 1948) exists in brachiopods is unknown, but the evidence amassed suggests that, if present, it is at best feebly developed. Similarly the deeper-water brachiopod larvae must be completely photonegative and not change during growth in this respect as described for some other invertebrates with

(16) Ref. Elliott (1948b).

a surface-layer phase by Thorsson (*op. cit.*, pp. 462–63), though photosensitivity is only a secondary evolutionary adaptation as compared with the duration of the larval stage.

It remains to consider the implications of terebratelloid evolution with regard to taxonomy. The history of the classification of terebratuloids and terebratelloids was reviewed by Thomson (1927, pp. 165–179). Briefly, the early concept of a terebratelloid genus as comprising those forms with a common pattern of loop was displaced when it was realised that such aggregates were polyphyletic and that the different stocks were indicated by the more slowly-evolving cardinalia. Subsequent practice has been to define a genus as comprising those forms within a cardinalian stock which have a common adult pattern of loop, the family and subfamily groupings being based on loop-development. This is convenient practice, although the writer has pointed out that it is possible for one species in such a genus to arise repeatedly from the parent stem at different times; two species in one genus may undergo parallel development into two comparable species in another genus¹⁷. Both these cases are at variance with the common unwritten concept of a genus as a group of related forms different in detail as a result of geographical or ecological migration, but expression of the difference taxonomically would make the nomenclature burdensome. It has been suggested that an investigation of the chromosomes and hybridisation—possibilities of brachiopods in one line of loop-progression would be of interest (Elliott, 1948, p. 312): certainly from the present point of view it would clearly indicate the degree of biological and hence of taxonomic importance to be attached to the pattern of adult loops. Meanwhile the existing practice outlined above is as good as any.

V. SUMMARY.

The species *Trigonosemus acanthodes*, *Magas mesembrinus* and *Magasella cretacea*, described by Etheridge (1913) from the Gingin Chalk, are now re-described in detail and referred by reason of their internal structure to the genera *Inopinatarcula* nov., *Kingena* Davidson and *Bouchardiella* Doello-Jurado respectively. The palaeogeographic significance of *Kingena* with regard to the Tethys, and of the occurrence of *Bouchardiella* both in Australia and S. America, is discussed: also the evolutionary significance of the stage at which an adult loop is attained in the former genus, and of the type of loop in the second genus. Finally, some fresh evidence bearing on brachiopod migration, and the implications of terebratelloid evolution on taxonomy, are reviewed.

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(17) The average of specific characters—shape, outline, adult size and colouration—changes from one species to another, genetically when new colonies are derived from a few individuals and also as a result of selection for the new environment. Thus subsidiary stocks based on specific characters, within cardinalian stocks, are not as a rule distinguishable though colour-patterning may persist (cf. Thomson, 1927, p. 291).

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KEY TO SYMBOLS ON PLATES I AND II.

a	= ascending branch	lev	= lateral cave
asc	= adductor muscle-scar	mcl	= median callus
bl	= bouchardiform lamella	mf	= median fold
br	= beak-ridge	mm	= muscle-mark
c	= crus	mr	= median ridge
cb	= crural base	ms	= median septum
cp	= cardinal process	mv	= median cavity
d	= descending branch	mx	= matrix
dbc	= connection from descending branch to septum	ohp	= outer hinge-plate
dl	= dental lamella	osr	= outer socket-ridge
dp	= deltidial plate	pat	= posterior attachment of loop
f	= foramen	pc	= pedicle-collar
dsc	= diductor muscle-scar	ps	= pallial sinus-mark
g	= groove of hinge-tooth	psc	= pedicle muscle-scar
h	= hinge-trough	pt	= pedicle tunnel
hpl	= hinge-platform	s	= hinge-socket
i	= interarea	sp	= spine
ihp	= inner hinge-plate	sy	= symphytium
isr	= inner socket-ridge	tb	= transverse band
iss	= slope of inner socket-ridge	tbc	= connection from transverse band to septum
ka	= posterior aperture of loop	te	= hinge-tooth
lc	= lateral beak cavity	tr	= muscle-trough

Explanation of Plates.

PLATE I.

Figs. 1-13. *Kingena mesembrina* (Etheridge). All from the Chalk (Senonian) of the Gingin District, Western Australia.

1. Brachial valve with loop from an individual of 8.25mm. shell-length, side view.
2. The same, posterior view.
3. The same, anterior view.
4. The same, seen from above.
5. Brachial valve with broken loop from an individual of 12mm. shell-length, lateral-oblique view.
6. Pedicle valve from an individual of 8.25mm. shell-length, anterior view.
7. Brachial valve, posterior half, with loop embedded in matrix; specimen of 21mm. shell-length.
8. Pedicle valve from a distorted individual of about 9mm. shell-length.
9. Brachial valve, posterior view of same specimen as in Fig. 7.
10. Brachial valve view of posterior portion of specimen of 10mm. shell-length.
11. Adult shell, side view.
12. Small variety, anterior view.
13. The same, brachial valve view.

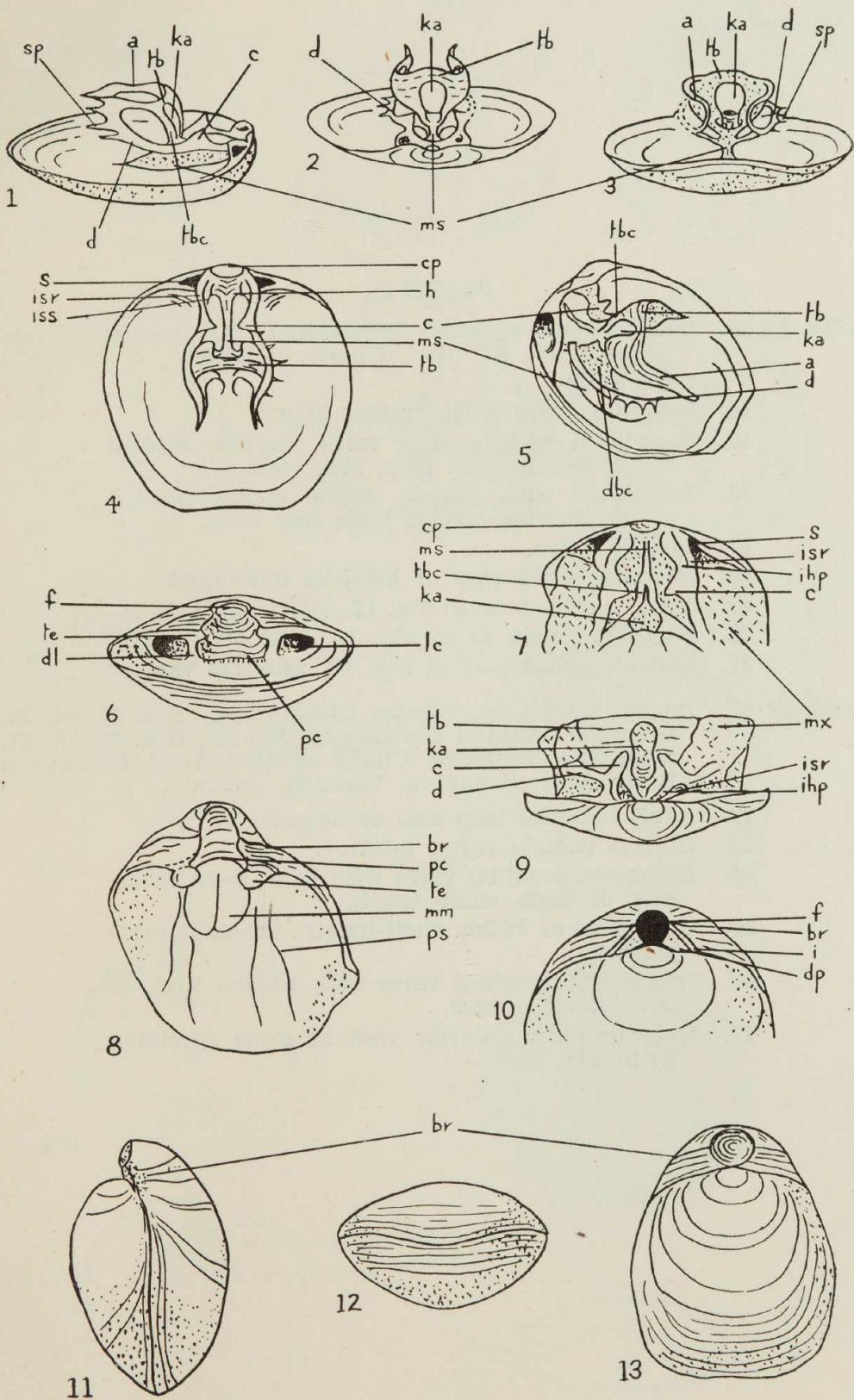


Plate I.

PLATE II.

Figs. 14-21. *Bouchardiella cretacea* (Etheridge). All from the Chalk (Senonian) of the Gingin District of Western Australia.

14. Brachial valve with broken loop.
15. Individual with pedicle valve mostly broken away, showing old loop, side view.
16. Individual with pedicle valve mostly broken away, showing earlier loop, side view.
17. Pedicle valve.
18. Brachial valve view of bivalved individual.
19. Same specimen as in Fig. 15, interior.
20. Same specimen as in Fig. 16, interior.
21. Same specimen as in Fig. 18, anterior view.

Figs. 22-27. *Inopinatarcula acanthodes* (Etheridge). Nos. 22, 24, 26, from the Chalk of the Gingin District; Nos. 23, 25, 27, from the Toolonga Chalk of the lower Murchison River Area: Senonian, Western Australia.

22. Adult brachial loop and cardinalia.
23. Broken pedicle valve, interior.
24. Immature brachial valve with loop, from specimen of 9mm. shell-length.
25. Individual of 16.5m. shell-length, brachial valve view.
26. Interior of brachial valve with broken loop, to show muscle-scars.
27. Diagrammatic anterior view of same specimen as in Fig. 25.

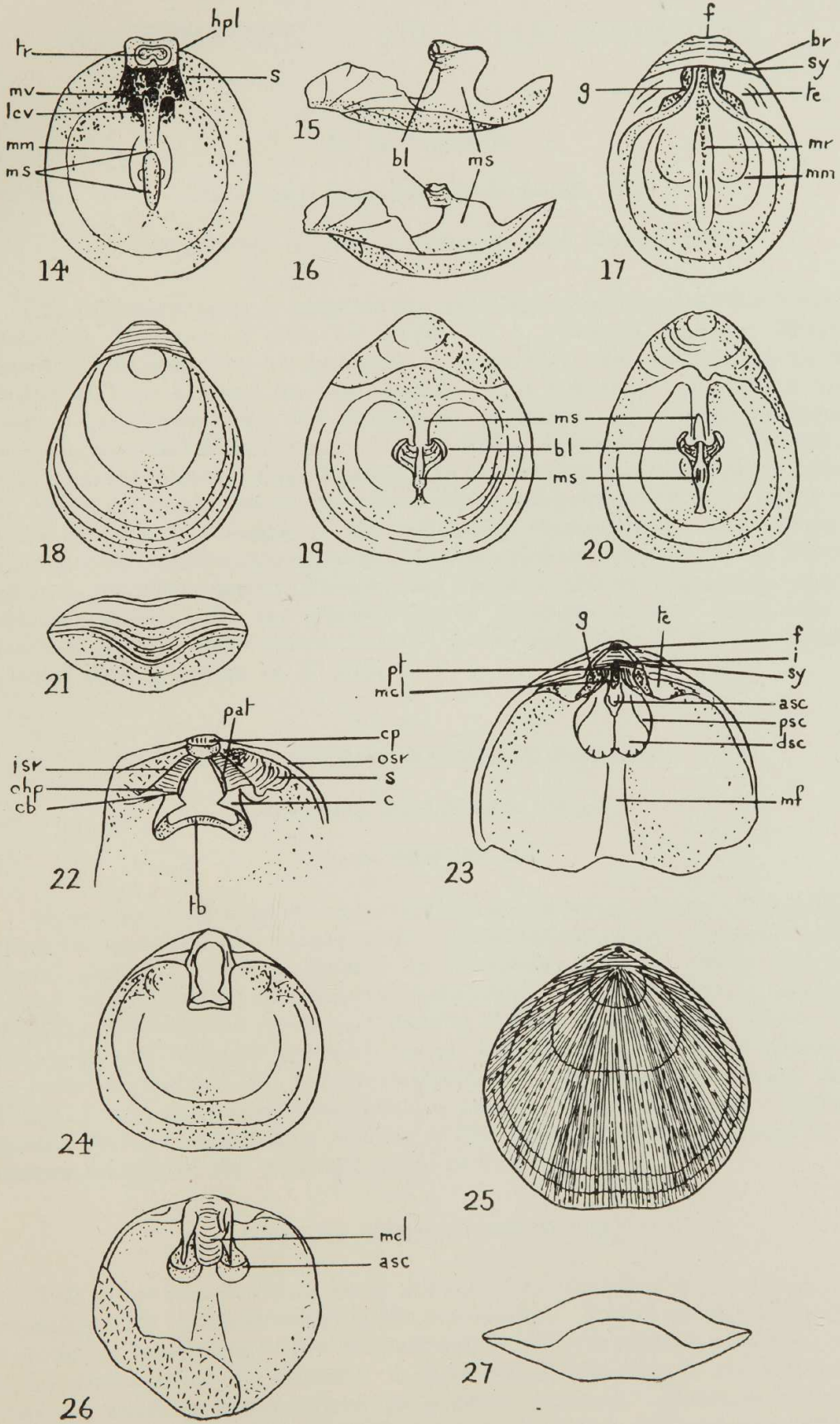


Plate II.